Viability Status of Oregon Salmon and Steelhead Populations in the Willamette and Lower Columbia Basins

Appendix F: PopCycle Model Description

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POPCYCLE MODEL DESCRIPTION

PopCycle is a simple stochastic salmon stock recruitment model for analysis of population viability. The model estimates annual spawner numbers over a 100-year period for a prescribed number of iterations (Figure 1). The model is initialized with recent population size and subsequent numbers are calculated using a stochastic stock-recruitment function described by input parameters. Recruits are estimated as an ocean adult cohort. Annual numbers of fish from this cohort are apportioned among years based on an input age schedule. The model includes optional inputs to apply fishing rates in each year to calculate harvest and fishery effects on population dynamics. Optional inputs are also included for analysis of demographic effects of natural spawning by hatchery fish based on inputs for hatchery releases, release to adult survival, and rates of natural spawning by hatchery fish. Risks were expressed based on probabilities of future spawning escapement less than prescribed threshold values. The model is built in Microsoft Excel using Visual Basic. A simple interface page facilitates model use and review of results.

Descriptions of derivation and application of model variables and inputs follow.

Conservation risks

This analysis estimates population viability based quasi-extinction and critical risk thresholds. A quasi-extinction threshold (QET) is defined as a population size where functional extinction occurs due to the effects of small population processes (McElhany et al. 2006). The model assumes that extinction occurs if the average annual population size over a generation (g) falls below this threshold at any point in a modeled trajectory. Quasi-extinction risk is thus estimated as the proportion of all iterations where the moving generational average spawner number falls below the QET at any point in each 100 year simulation. Estimated risks are compared to benchmark values of 60% 25%, 5%, and 1% risk levels identified by the Willamette/Lower Columbia Technical Recovery Team (McElhany et al. 2006) as corresponding to high, moderate, low, and very low extinction risks.

The analysis also considers risks of falling below a conservation risk threshold (CRT) that is greater than the assumed quasi-extinction level. The CRT level might be considered analogous to a point where a population is threatened with falling to lower levels where the risk of extinction becomes significant. For the purposes of this analysis, CRT is defined as a level where diversity is eroded and population resilience may be lost. CRT may be considered to be the risk of being threatened with becoming endangered with quasi-extinction.

Population-specific estimates of extinction risks and improvement scalars were based on QET values of 50 for all populations and CRT values ranging from 50 to 300 depending on species and the size of the basin inhabited by a population (McElhany et al. 2006). While there is an extensive amount of literature on the relationships among extinction risk, persistence time, population abundance, and level of variation in demographic parameters, there are no simple generic abundance levels that can be identified as viable (McElhany et al. 2000). Because empirical data on actual extinction and conservation risk levels is lacking, QET and CRT values were based on theoretical numbers identified in the literature based on genetic risks. Effective population sizes between 50 to 500 have been identified as levels which theoretically minimize risks of inbreeding depression and losses of genetic diversity, respectively (Franklin 1980, Soule 1980, Thompson 1991, Allendorf et al. 1997). Effective population size assumes balanced sex ratios and random mating. Benchmark values in this analysis assume approximately equivalent effects of differences between effective and census population sizes, and the multi-year generation structure of salmon (Waples 1990, 2004; Lindley et al. 2007). Relatively low QET values are supported by recent observations of salmon rebounds from very low numbers (e.g. Oregon lower Columbia River coho: ODFW 2005 and Washington lower Columbia winter steelhead: D. Rawding, WDFW, unpublished) and apparently-sustainable small population sizes of salmon in other regions (e.g. King Salmon River Chinook population in Alaska: McPherson et al. 2003).

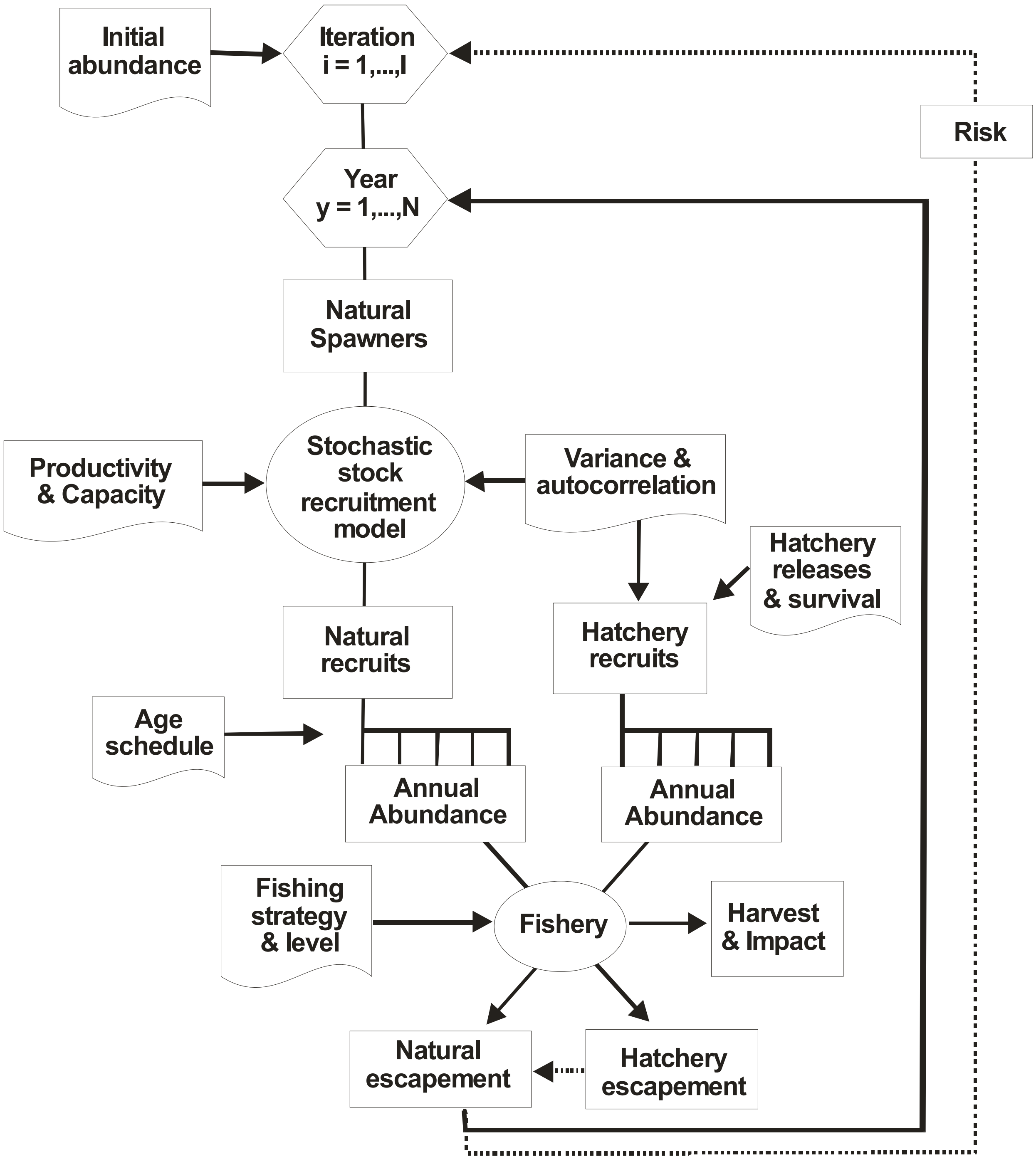

Figure 1. **Model algorithm.**

Stock-Recruitment Function

The model stock recruitment function can be based on either hockey stick, Beverton-Holt, or Ricker functional forms.

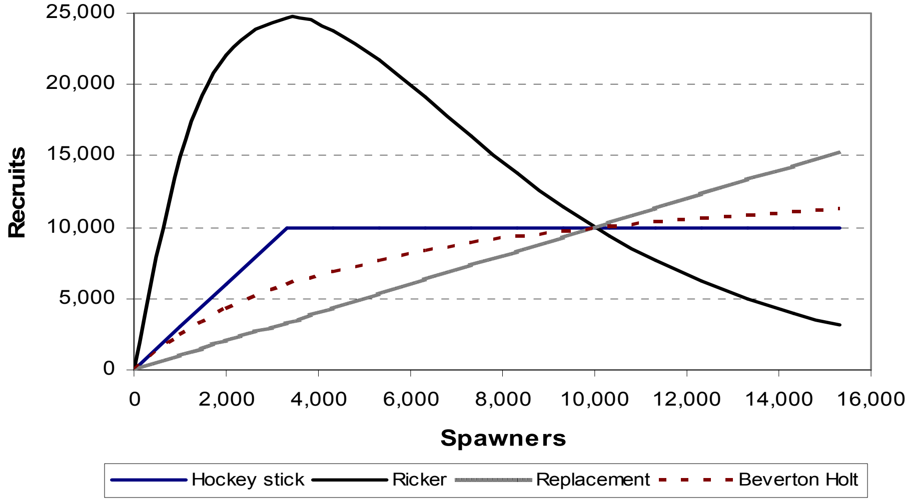

Figure 2. Example stock-recruitment curves based on a productivity parameter of 3 recruits per spawner (maximum observed at low numbers) and an equilibrium population size of 10,000.

The Hockey Stick form of the relationship is:

$$R_y = (S_y)(\,p)\,(e^{\varepsilon}) \text{ when } (S_y)(p) < N_{eq}$$
$$R_y = (N_{eq})\,(e^{\varepsilon}) \text{ when } (S_y)(p) \geq N_{eq}$$

where

R_y = recruits,
S_y = spawners,
p = parameter for productivity (average recruits per spawner at spawner numbers under full seeding levels),
N_{eq} = parameter for equilibrium abundance,
e = exponent, and
ε = normally-distributed error term ~ $N(0, \sigma^2)$

The Beverton-Holt form of the relationship is:

$$R_y = \{a\,S_y / [1 + (S_y\,(\,a\,-1)/\,N_{eq})]\}\;e^{\varepsilon}$$

where

R_y = recruits,
S_y = spawners,
a = productivity parameter (maximum recruits per spawner at low abundance),
N_{eq} = parameter for equilibrium abundance,
e = exponent, and
ε = normally-distributed error term ~ $N(0, \sigma^2)$.

The Ricker form of the relationship is:

$$R_y = S\,e^{\,\alpha\,[1-(S/Neq)]\;+\,\varepsilon}$$

where

R_y = recruits,
S_y = spawners,

α = Ricker productivity parameter (maximum recruits per spawner at low abundance),
N_{eq} = parameter for equilibrium abundance,
e = exponent, and
ε = normally-distributed error term.

Population-specific assessments of risk and improvement scalars were based on the best available data for each population. Population-specific stock-recruitment parameters where used where available. Parameters were based on a hockey stick formulation and the mean RS approach identified by McElhany et al. (2006). This approach defines the equilibrium abundance based on the median pre-harvest recruitment level observed in the historical data time series. The productivity parameter was based on the geometric mean of recruits per spawner for spawning escapements less than the median value in the data set. Pre-harvest stock-recruitment data was used to estimate intrinsic population parameters to account for significant and well documented changes in harvest patterns over time. Population parameters were inferred from habitat conditions in many cases where population-specific stock recruitment data were unavailable. Habitat inferences were generally based on the Ecosystem Diagnosis and Treatment Model (LCFRB 2005). EDT results are in the form of Beverton-Holt function parameters. Note that MeanRS and Beverton-Holt equilibrium and productivity parameters are related but not directly comparable. Where specific population data were lacking, representative values were used consistent with the assumed population status based on other anecdotal information.

Analyses were based on initial population sizes equal to the average equilibrium abundance as specified with the corresponding stock recruitment parameter (N_{eq}). Equilibrium rather than recent abundance levels were used to provide estimates of representative long term risks and avoid confounding effects of large annual fluctuations in spawner escapements in recent years. For instance, viability estimates based on record low escapements during poor El Niño conditions of the late 1990s would have resulted in different results than would have been calculated from recent high returns associated with a post El Niño transition to more favorable ocean conditions. Additional sensitivity analyses were conducted to examine the effect of initial abundance on risks, particularly including near term risks.

Stock-Recruitment Variance

The stochastic simulation model incorporated variability about the stock-recruitment function to describe annual variation in fish numbers and productivity due to the effects of variable freshwater and marine survival patterns (as well as measurement error in stock assessments). This variance is modeled as a lognormal distribution (e^{ε}) where ε is normally distributed with a mean of 0 and a variance of σ_z^2 (Peterman 1981).

The model allows for simulation of autocorrelation in stock-recruitment variance as follows:

$$Z_t = Ø\, Z_{t-1} + \varepsilon_t, \qquad \varepsilon_t \sim N(0, \sigma_e^2)$$

where

Z_t = autocorrelation residual,
Ø = lag autoregression coefficient,
ε_t = autocorrelation error, and
σ_e^2 = autocorrelation error variance.

The autocorrelation error variance (σ_e^2) is related to the stock-recruitment error variance (σ_z^2) with the lag autoregression coefficient:

$$\sigma_e^2 = \sigma_z^2\,(1 - Ø^2)$$

Model simulations using the autocorrelated residual options were seeded in the first year with a randomly generated value from N(0, σ_z^2).

Variance and autocorrelation in population-specific risk analyses were generally based on species values reported by McElhany et al. (2006), except where good population-specific estimates were available for long term datasets.

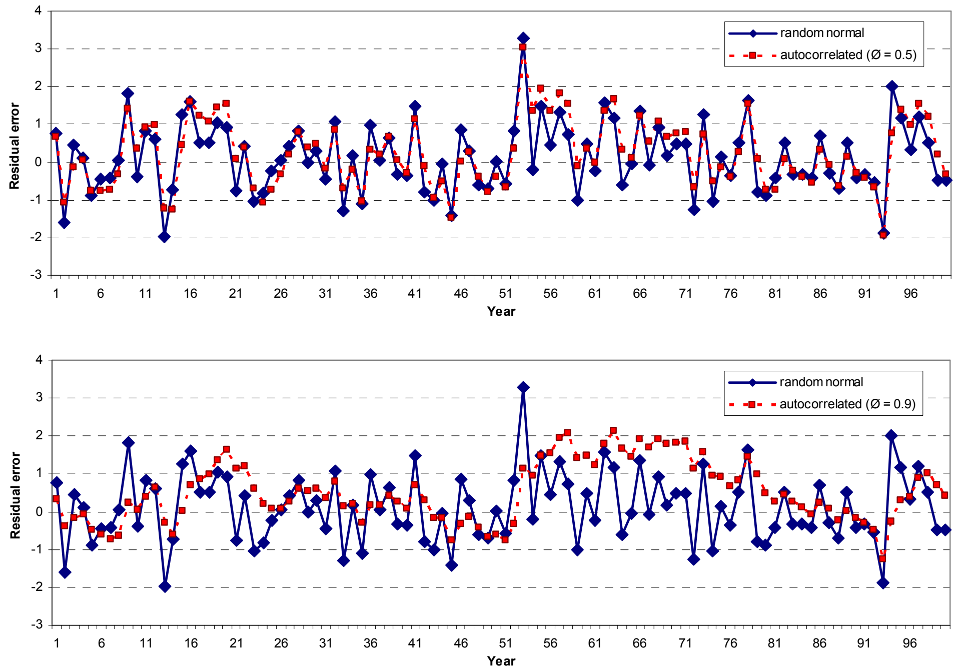

Figure 3. Examples of autocorrelation effect on randomly generated error patterns (σ_z^2 = 1).

Depensation & Recruitment Failure Thresholds

The model provides options to limit recruitment at low spawner numbers consistent with depensatory effects of stock substructure and small population processes. Options include 1) progressively reducing productivity at spawner numbers below a specified recruitment depensation threshold (RDT) and/or 2) setting recruitment to zero at spawner numbers below a specified recruitment failure threshold (RFT):

$$R' = R * (1 - \mathrm{Exp}((\mathrm{Log}(1 - 0.95) / (RDT - 1)) * S)) \text{ when } S > RFT$$

$$R' = 0 \text{ when } S < RFT$$

where

R' = Number of adult recruits after depensation applied,
R = Number of adult recruits estimated from stock-recruitment function,
S = spawners, and
RDT = Recruitment depensation threshold (spawner number).

Population-specific analyses were based on a RFT of 50 and a recruitment depensation threshold equal to the CRT.

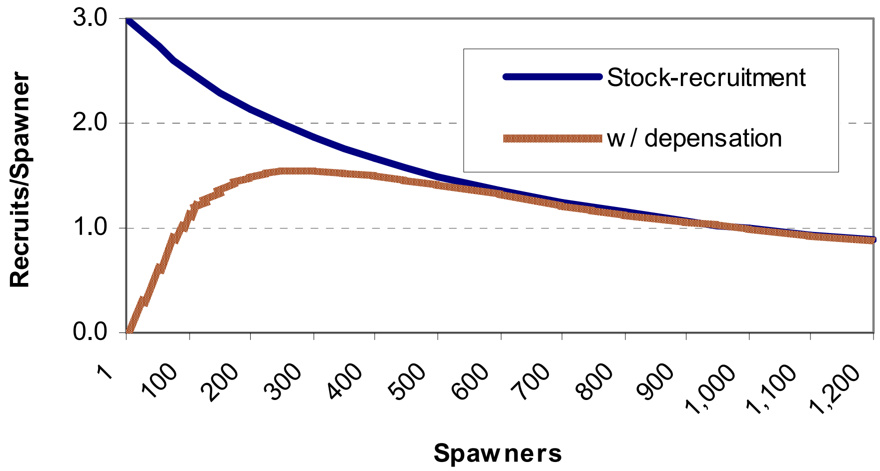

Figure 4. Example of depensation function effect on recruits per spawner at low spawner numbers based on a Beverton-Holt function (a = 3.0, Neq =1,000, γ =500).

Production Trend

The model includes an optional input to allow average productivity to be annually incremented upward or downward so that effects of trends in habitat conditions might be considered:

$$R'' = R' (1 + t)^y$$

where

R' = Number of adult recruits after depensation applied, and
t = proportional annual change in productivity.

McElhany et al. (2006) assumed a median annual decline of ln(y) = 0.995 to future simulations based on a precautionary expectation of declining snow packs, survival indices, and climate change. Population-specific analyses included in this analysis assumed a long-term trend equivalent to a 20% reduction in net productivity over 100 years.

Improvement Scalar

The model includes an optional scalar which is used to estimate the effects of incremental improvements in realized recruitment on quasi-extinction risks:

$$R^* = R'' (1 + C/100)$$

where

C = Improvement scalar (%), and
R* = Number of adult recruits after application of the improvement scalar.

Note that application of an improvement scalar results in a proportion increase in equilibrium population size and productivity at spawner numbers less than the equilibrium value (Figure 5). Population-specific improvement scalars will be used in future applications to represent increments needed to reach prescribed risk levels (1%, 5%, 25%) relative to a baseline at the time of the original ESA listing.

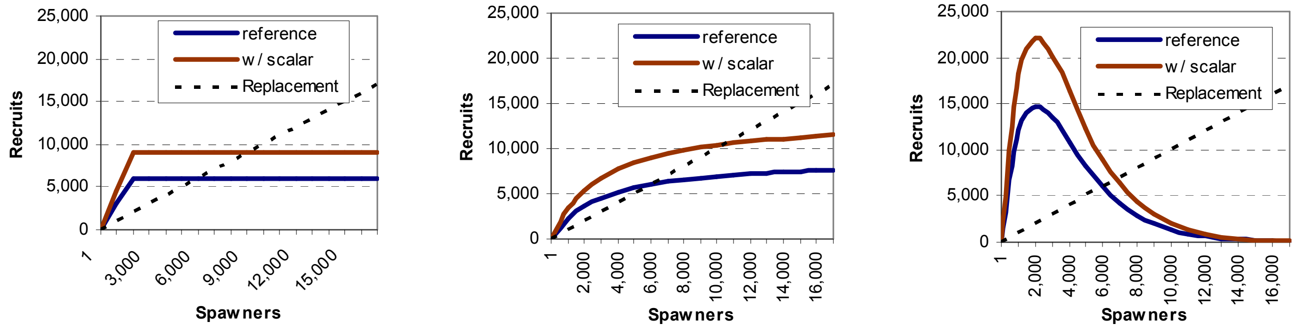

Figure 5. **Example of effects of improvement scalar (50%) on hockey stock, Beverton Holt, and Ricker stock-recruitment relationships based on an equilibrium abundance of 6,000 and a productivity parameter of 3 recruits per spawner.**

<u>Annual Abundance</u>

Numbers of naturally-produced fish ($N_{.y}$) destined to return to freshwater in each year are estimated from a progressive series of recruitment cohorts based on a specified age composition:

$$N_{.y} = \Sigma\, N_{xy}$$

$$N_{xy} = R^*_{y-x}\, m_x$$

where

N_{xy} = Number of mature naturally-produced adults of age x destined to return to freshwater in year y, and

m_x = Proportion of adult cohort produced by brood year spawners that returns to freshwater in year x

Species-specific age schedules were based on unpublished WDFW data for fall Chinook (1980-2004 lower river tule returns) and average values estimated for other species in McElhany et al. (2006). McElhany et al. (2006) numbers were revised to include jack proportions for coho (age 2) based on Clackamas and Sandy River data and spring Chinook (age 3) based on McKenzie, Clackamas, and Sandy River data. Jacks were included to reflect their genetic contributions to effective population sizes.

Table 1. **Average spawner age composition based on escapement data available for Willamette and lower Columbia salmon populations (McElhany et al. 2006 and WDFW unpublished).**

Species	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6	Age 7	Generation (yrs)
Coho	0	0.05	0.95	0	0	0	0	3
Spring chinook	0	0	0.05	0.54	0.40	0.01	0	4
Fall chinook	0	0.06	0.42	0.46	0.06	0.00	0	4
Chum	0	0	0.41	0.57	0.02	0	0	4
Steelhead	0	0	0.01	0.45	0.42	0.11	0.01	5

<u>Hatchery Fish</u>

The model includes option inputs for modeling co-occurring natural and hatchery populations. Number of hatchery-produced fish ($H_{.y}$) destined to return to freshwater in each year is estimated based on input juvenile release numbers (J), release-to-adult survival rates (SAR), and age composition (m_x):

$$H_{.y} = \Sigma\, H_{xy}$$

$$H_{xy} = (J)(SAR)(e^{\varepsilon})(m_x)$$

where

H_{xy} = Number of mature hatchery-produced adults of age x destined to return to freshwater in year y

Note that the model incorporates random normal variation in hatchery survival rates among release cohorts using a scalar based on natural productivity derived from the stock-recruitment variance. Thus, hatchery and natural numbers varied in strict tandem. The corresponding assumption would be that variation in hatchery and wild production was highly correlated due to common effects of freshwater and marine factors. Hatchery fish were not modeled in this risk analysis.

Fisheries & Harvest

Annual numbers are subject to optional fishing rates. This option is useful for adjusting future projections for changes in fisheries and evaluating the effects of alternative fishing strategies and levels. Fishery impact is defined in the model in terms of the adult equivalent number of fish that die as a result of direct and indirect fishery effects:

$$IN_y = N_{.y} fN_y \quad \text{and} \quad IH_y = H_{.y} fH_y$$

where

IN_y = fishery impact in number of naturally-produced fish,
fN_y = fishery impact mortality rate on naturally produced fish including harvested catch and catch-release mortality where applicable,
IH_y = Fishery impact in number of hatchery-produced fish, and
fH_y = fishery impact mortality rate including harvested catch and other mortality where applicable.

Estimates of population-specific risks were based on pre-harvest stock-recruitment parameters calculated using fishery harvest rates representative of current conditions: 25% for coho, 25% for spring Chinook, 50% for fall Chinook, 50% for late fall Chinook, 5% for chum, and 10% for steelhead. Rates include ocean and freshwater fisheries and represent management practices in years prior to listing (intended to reflect conditions that led to status at the time of listing). Note that conservation measures implemented since listing have further reduced fishing rates from historical levels.

Spawning Escapement

Estimates of natural spawning escapement (S_y) include naturally-produced fish that survive fisheries plus a proportion of the hatchery escapement that spawns naturally decremented by the relative spawning success of a hatchery fish:

$$S_y = SN_y + SH_y$$

$$SN_y = (N_{.y} - IN_y)$$

$$SH_y = (H_{.y} - IH_y)\, q\, \tau$$

where

SN_y = Naturally-produced spawners in year y,
SH_y = Hatchery-produced natural spawners in year y,
q = proportion of hatchery escapement that spawns naturally, and
τ = spawning success of a naturally-spawning hatchery fish relative to that of a naturally-produced spawner.

The model also tracks the proportion of natural influence by hatchery fish (pNI)::

$$pNI_y = SH_y / S_y$$

Note that the relative fitness of a hatchery spawner is applied only to first generation hatchery spawners and continuing hatchery fitness effects in subsequent generations are to be represented in model applications by changes in stock-recruitment parameters.

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